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Differential development of breeding plumage in adult and second-year male Ruffs *Philomachus pugnax*

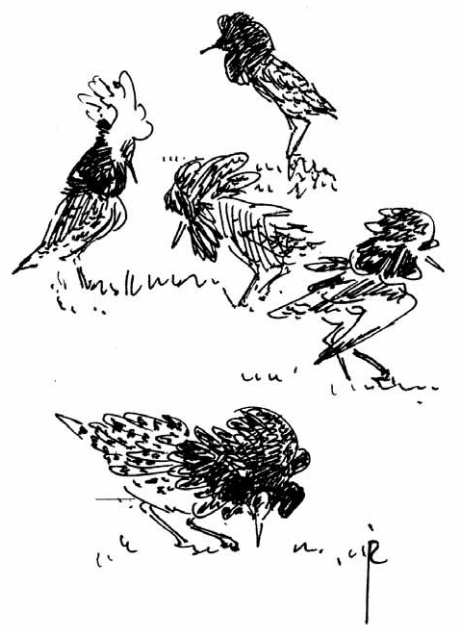
Natalia Karlionova[1], Włodzimierz Meissner[2,*] & Pavel Pinchuk[1]

Karlionova N., Meissner W. & Pinchuk P. 2008. Differential development of breeding plumage in adult and second-year male Ruffs *Philomachus pugnax*. Ardea 96(1): 39–45.

We studied the development of breeding plumage in 641 Ruff *Philomachus pugnax* males during spring in 2004–2006 in southern Belarus with special emphasis on the growth rate of ruff and tuft feathers, which are the most colourful and spectacular parts of the male plumage. During northward migration, male Ruffs arriving in the end of March or early April showed a mixture of winter and striped feathers. The first adults with fully developed breeding plumage were recorded in the last 10 days of April and the proportion of individuals with breeding plumage gradually increased through spring. However, individuals with at least traces of winter or striped plumage were caught during the whole study period. Birds did not shed the whole winter plumage at once, which is typical for Ruff males in western Europe. Immature (second year) birds were less advanced in developing breeding plumage than adults. Only 20% of all 55 trapped second-year males were in full breeding plumage. During the main migration period there were no annual differences in the growth rate of breeding plumage feathers. Ruff lengths increased 1.6 mm/day in adults and 1.5 mm/day in second-year males, whereas the tuft grew 1.1 mm/day in adults and 1.0 mm/day in immatures. Although growing rates of ruff and tuft feathers were similar in immatures and adults, immature males started to moult into breeding plumage later than adults, resulting in less developed breeding plumage when they departed to the breeding grounds. As second-year males had lower body mass and slower body mass increase than adults, it was proposed that energetic constraints during migration are the main reason of delayed moult into breeding plumage in immature birds.

Key words: Ruff, moult, breeding plumage, body mass, spring migration

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INTRODUCTION

In many waders, immature (second-year) males develop full breeding plumage later than adults or exhibit an incomplete moult (Kozlova 1961, Prater *et al.* 1977). The Ruff *Philomachus pugnax*, a lekking species, has three plumages during the year. Before northward migration from the African wintering grounds, males and females undergo a partial moult from winter into alternate (striped) plumage, which is replaced later by supplemental (breeding) plumage (Jukema & Piersma 2000).

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The breeding plumage has bright coloured ornamental feathers grown on the males' neck and head, called ruff and tufts, respectively. Ruffs moult into their breeding plumage at stopovers during migration. Examination of moult and plumages of Ruffs has been conducted in different wintering and stopover sites (Kozlova 1961, Stresemann & Stresemann 1966, Schmitt & Whitehouse 1976, Pearson 1981, Koopman 1986, OAG Munster 1991, Jukema *et al.* 1995, Jukema & Piersma 2000, Jukema *et al.* 2001), but quantitative data on the growth rate of breeding plumage feathers are missing. It remains to be studied if Ruffs stopping over in different regions of Europe show similar timing of plumage changes, especially as birds wintering in various regions of Africa seem to use different flyways (Underhill *et al.* 1999). During spring migration through Europe, second-year Ruff males are less advanced in prebreeding moult that adult males (van Rhijn 1991). This difference might be a result of a later onset of moult in second-year birds, a lower growth rate of feathers in young males, or a combination of both. The aim of this paper, therefore, is to describe the development of breeding plumage in Ruff males during spring migration through southern Belarus, and to compare growth rate of ruff and tuft feathers of second-year and adult birds.

METHODS

In years 2004–2006, Ruffs were captured in the floodplain meadows of the Pripyat Valley in walk-in traps (Meissner 1998) placed on small islands; mist-nets were used occasionally. All catches were made near Turov town (Gomel Region, 52°04' N, 27°44' E). This place is an important stopover site for waders during spring and autumn migration, in particular for the Ruff with spring concentrations of 10–14 thousand in the end of April or early May. A detailed description of the study area is given in Pinchuk *et al.* (2005).

Two age classes were distinguished: second-year birds (hatched in the previous year) and adults. The age of the captured birds was defined by the presence (or absence) of juvenile inner median coverts (Prater *et al.* 1977), leg colour and the stage of wear of primaries (Schmitt & Whitehouse 1976, Meissner & Scebba 2005).

A small sample of 2–5 of the longest feathers was plucked from each bird (n = 641) and stored in numbered envelopes. The feathers were sampled from just inside the colourful ruff and tuft on the left side of the bird. The maximum length of the longest feather from quill base to the vane tip was measured with a stopped ruler with an accuracy of 0.5 mm. Three types of feathers (from winter, striped or breeding plumage) were distinguished according to Jukema & Piersma (2000). The extent of different plumages was estimated on the basis of digital photographs (n = 291) of breast and head of each Ruff male. The photographs were taken only in 2005 and 2006, while the samples of feathers were collected during the whole research period. Birds were classified into one of three categories: (1) with feathers from winter and striped plumages, with no traces of breeding plumage; (2) with a mixture of winter or striped feathers and breeding plumage; (3) exclusively in breeding plumage.

Birds were weighed with an accuracy of 1 g. Data on lengths of ruff and tuft feathers and on extent of different plumages were not collected simultaneously in all birds, thus the sample sizes in different analyses were not equal.

The first males arrive at Turov in mid-March or early April, but the majority of males pass through the area between 20 April and 10 May (own unpubl. data). For comparison of the mean length of ruff and tuft feathers between seasons, only data from this period were taken into account. All statistical methods used in this study followed Zar (1996) and Statsoft (2001). The analyses were done in STATISTICA 6.0 software (StatSoft 2001).

RESULTS

During northward migration, adult male Ruffs arrived earlier than second-year birds (Fig. 1). In the end of March or beginning of April, when

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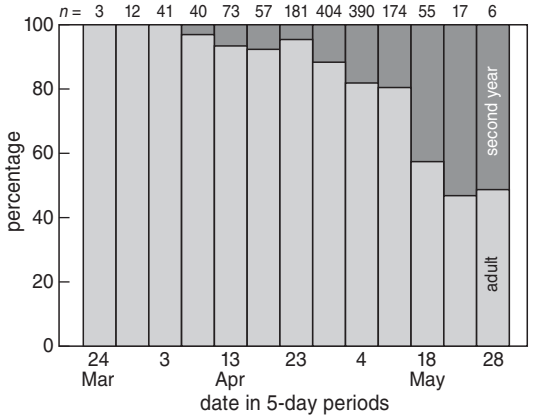


Figure 1. Seasonal changes in the percentage of adult and second-year Ruff males in catches. Data from 2005 and 2006 were combined, and grouped into a standard scheme of 5-day periods (Berthold 1973). The middle date of each period is presented. Sample sizes are given above.

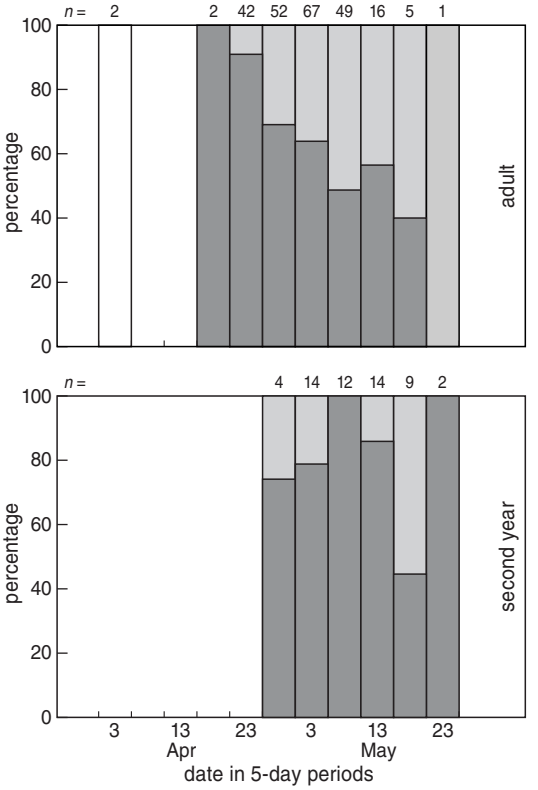


Figure 2. Seasonal changes in the percentage of plumage categories in adult (upper panel) and second-year (lower) Ruff males. White bar= mixture of winter and striped plumage, dark grey bar= mixture of winter or striped and breeding plumages, light grey bar= breeding plumage exclusively. Data from 2005 and 2006 were combined and grouped into a standard scheme of 5-day periods (Berthold 1973). The middle date of each period is presented. Sample sizes are given above bars.

probably only adults stayed in the study area, Ruff males showed a mixture of winter and striped feathers. This assessment was mainly based on observing birds at a distance as only two birds were caught in this period (Fig. 2). The first adults with full breeding plumage were recorded in the end of April, with a continuous increase in proportion of males in breeding plumage since then. Individuals with traces of winter or striped plumage were caught during the whole study period (Fig. 2). Apparently the moult of neck feathers was gradual, and only few of the feathers were replaced at a same time as we observed only some birds with small parts of the neck without feathers at all. Second-year birds were less advanced in developing breeding plumage than adults. Between 26 April and 20 May, when both age classes were abundant, 21% (n = 53) of second-year males were in full breeding plumage, which was significantly less than in adults (40%, n = 189) ($\chi^2 = 6.47, P = 0.01$).

Despite slight differences between seasons in the beginning of spring migration, the mean length of ruff and tuft in males caught within the main migration period in subsequent years showed no significant difference (ANOVA, ruff: $F_{2,507} = 0.16$, $P = 0.85$; tuft: $F_{2,507} = 0.79$, $P = 0.46$). Thus, data from all years were combined. There were significant, positive correlations between the date and the length of ruff and tuft in both age classes (Fig. 3). The length of ruff increased 1.6 mm day^{-1} in adults and 1.5 mm day^{-1} in second-year males, whereas the tuft grew 1.1 mm day^{-1} in adults and 1.0 mm day^{-1} in second-year birds. To check for differences between both age classes in growing rates of the ruff and the

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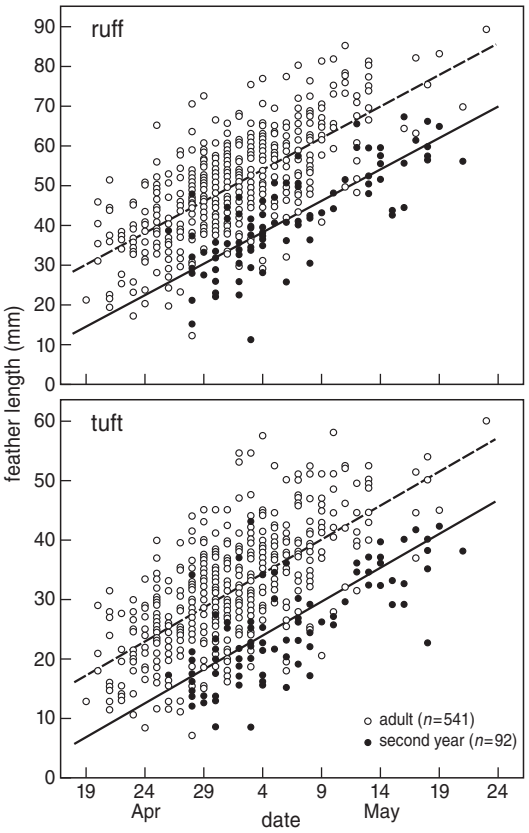


Figure 3. Seasonal growth of ruffs and tufts in adult (and second-year males Ruffs caught in the Pripyat Valley in Belarus. Dotted lines are linear regression of feather length and date in adults, solid lines indicates second-year birds. Lines are based on ANCOVA mentioned in text.

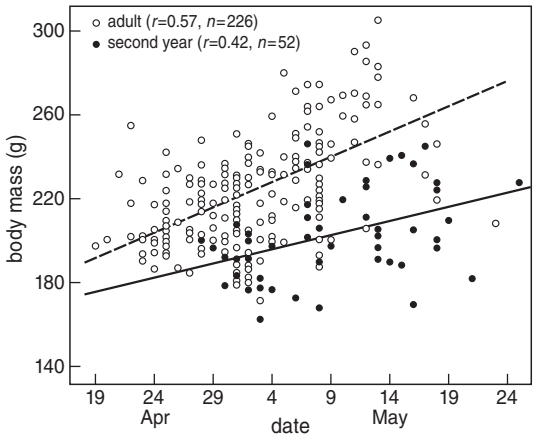


Figure 4. Seasonal body mass changes in adult and second-year males Ruffs caught in the Pripyat Valley in Belarus. Dotted line represents linear regression in adults, solid line indicates second-year birds.

tuft, one-way ANCOVA was performed with age as factor and date as a covariate. The only significant factor was date (ANCOVA, ruff: $F_{1,629} = 362.8$, $P < 0.0001$; tuft: $F_{1,629} = 269.9$, $P < 0.0001$). The influence of age was not significant (ANCOVA testing for difference in slope, ruff: $F_{1,629} = 1.7$, $P = 0.19$; tuft: $F_{1,629} = 0.1$, $P = 0.74$). Thus, we could not detect an age class difference in growth rates of ruff and tuft. However, the ornamental feathers were longer in adults than second-year birds (ANCOVA, ruff: $F_{1,630} = 233.0$, $P < 0.0001$; tuft: $F_{1,630} = 187.4$, $P < 0.0001$). Based on the ANCOVA, we conclude that adult and second-year males started moulting ruff and tuft feathers in the beginning of April and the end of the first 10-day period in April, respectively.

The body mass of adult and second-year males increased during the season (Fig. 4). This increase was faster in adults (ANCOVA testing for difference in slopes, $F_{1,273} = 72.7$, $P < 0.0001$), and adults had a higher mean body mass than second-year birds during their stay in the study area (adults: mean 221.4 g ± 24.8 SD, $n = 1245$; second-years: mean 196.9 g ±18.7 SD, $n = 194$; Cochran-Cox test, $t' = 16.2$, $P < 0.0001$).

DISCUSSION

The growing rates of ruff and tuft feathers were similar in second-year and adult Ruffs, but in second-year males breeding plumage development starts later than in adults. Our results are in agreement with published data on the timing of moult in Ruffs. Between January and April, Ruffs start to develop striped plumage, but winter plumage is still partly retained at this time. Breeding plumage feathers occur during spring migration at temper-

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ate breeding sites (Cramp & Simmons 1983, Jukema & Piersma 2000). In The Netherlands, the first Ruff males caught between early March and early April show a mixture of winter and striped plumages with only few feathers of breeding plumage (Jukema & Piersma 2000). However one month later, in early May, an average 80% of breast feathers sampled from males belong to breeding plumage (Jukema & Piersma 2000). Similarly, in the southern part of the former USSR, the first Ruffs appear in March without or with only partially developed ruffs (Dementiev & Gladkov 1951). It is worth noticing that in Belarus, even in mid-May 30–40% adult males still had traces of winter feathers and/or striped feathers, and this proportion was much higher than in The Netherlands at the same period, where not more than 20% showed a mixture of different plumages (Jukema & Piersma 2000). This discrepancy might be a methodological rather than biological difference. In the Dutch samples, feathers were plucked from the middle part of the breast. It is possible that very small traces of winter or striped feathers might be missed, especially since they were sampled only in one region of the breast, whereas small number of feathers contrasting with bright coloured breeding plumage may be still visible on photographs made in Belarus. On the other hand, feathers from breeding plumage are larger in size (mean 68.1 mm, range 65–70 mm, $n = 43$; own data) than those from striped or winter plumage (mean 23.6 mm, range 20–25 mm, $n = 30$; see also Fig. 2A in Jukema & Piersma 2000), hence some of the shorter feathers of the winter and striped plumage may be fully covered by others and they might be invisible on photographs, especially when they are present in small number. Likewise, we cannot exclude the possibility that differences in proportion of birds in fully developed breeding plumage between Belarus and The Netherlands reflects passage of Ruffs from different populations. A hint into this direction is our observation in early April of only about 5% of males with bare patches in the neck, which is in contrast to the Dutch Ruff males in spring which exhibit a more extensive moult of neck feathers (T. Piersma, pers. comm.). However, more data is needed from other parts of Europe to understand migration patterns through the continent.

Second-year males were less advanced in moulting into breeding plumage than adults. This is consistent with van Rhijn's (1991) observations that second-year males usually develop breeding plumage somewhat later. Some authors (Prater *et al.* 1977, Cramp & Simmons 1982) mentioned that in second-year males the breeding plumage is not fully developed or even absent (Kozlova 1961). Advancement in development of the breeding plumage is thought to be a signal of the nutritional status of an individual (Piersma & Jukema 1990, Piersma *et al.* 2001). Poor body condition and time constraints during migration may negatively affect timing of body moult, because moulting body feathers requires energy and impairs migratory fattening (Merilä 1997, Pérez-Tris *et al.* 2001). Consequently, second-year males have shorter ruff feathers than adults (Prater *et al.* 1977) and many second-year males belong to the group of marginal males on the leks (van Rhijn 1991), which are frequently attacked by territorial males, rarely win fights (Widemo 1998) and rarely copulate (van Rhijn 1991).

There were no detectable differences in growth rate of feathers between second-year and adult Ruff males, thus apparently the shorter tuft and ruff feathers in second-year birds are the result of a later start of moult. This might be a consequence of a generally lower foraging proficiency of young waders in comparison to adults, which results in slower spring migration and later arrival at the breeding grounds (Hockey *et al.* 1998). Indeed, second-year Ruff males arrive to Belarus later and they have significantly lower body mass and lower body mass increase during the season than adults (Fig. 3). As an alternative explanation, the delay might be adaptive. First, younger males might delay the onset of migration and feather growth to lower their threat status towards older males. By doing so, they avoid head-on competition with older, more experienced and settled males. Secondly, because display feathers are dropped very rapidly once the mating season is over

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(Cramp & Simmons 1982), second-year males might carry the feathers for a shorter total period of time than adults. In this way, young males reduce the costs of carrying them.

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SAMENVATTING

De auteurs bestudeerden de ontwikkeling van het broedkleed van 641 mannetjes Kemphaan *Philomachus pugnax* gevangen tijdens de voorjaarstrek in de jaren 2004–2006 in Wit-Rusland. Zij besteedden daarbij speciale aandacht aan de groeisnelheid van de kop- en kraagveren, de meest kleurrijke delen van het mannelijke kleed. De Kemphanen hadden bij aankomst eind maart – begin april een gemengd kleed van winterveren en gestreepte veren. De eerste volwassen mannetjes met een volledig ontwikkeld broedkleed werden waargenomen in de laatste tien dagen van april. Het aandeel mannetjes met volledig broedkleed nam toe in de tijd. Echter, gedurende de gehele studieperiode werden individuen gevangen met sporen van winterkleed en gestreepte veertjes. Onvolwassen vogels in hun tweede kalenderjaar vertoonden een minder ver ontwikkeld broedkleed dan adulte mannetjes. Van de 55 gevangen tweedejaars mannetjes had slechts 20% een volledig uitgegroeid broedkleed. De auteurs vonden geen significante verschillen tussen jaren in de gemiddelde lengte van de kraag- en kopveren van mannetjes gevangen tijdens de piekperiode van de trek. De veren groeiden dus elk jaar op ongeveer hetzelfde tijdstip uit. Ze zagen wel een significant positief verband tussen datum en de lengte van de kop- en kraagveren in beide leeftijdsgroepen. Tijdens de voorjaarstrek groeide de kraag met 1,6 mm per dag bij adulte vogels en 1,5 mm per dag bij tweedejaars vogels. De kopveren groeiden respectievelijk 1,1 mm en 1,0 mm per dag. De groeisnelheid van de veren in de twee groepen verschilt dus niet zoveel, maar tweedejaars beginnen waarschijnlijk later met ruien dan de adulte vogels en hebben dus een minder ver ontwikkeld broedkleed als ze vertrekken naar de broedgebieden. De auteurs veronderstellen dat energetische beperkingen tijdens de trek een reden kunnen zijn voor de verlate rui in tweedejaars vogels. Het feit dat de jongere vogels ook een lager lichaamsgewicht hadden en minder snel in gewicht toenamen, ondersteunt voornoemde hypothese. (YIV)

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